The effects of locality, season and year of seed collection on the germination of bugweed (*Solanum mauritianum* Scop.) seeds

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The germination requirements of bugweed (*Solanum mauritianum*) seeds are highly variable and appear to be influenced by locality and season of collection. Generally, bugweed seeds do not exhibit primary dormancy, but as fruits are produced throughout the year most will be subjected to climatic conditions which make them conditionally dormant. Seeds collected from the Natal Midlands showed a higher frequency of conditional and secondary dormancy than seeds from the other three localities. Irrespective of locality, seeds tended to exhibit the greatest secondary dormancy when collected during warmer months. Many seeds will therefore escape pre- and post-emergent herbicide treatments which are normally applied during this time.

Die ontkiemingsvereistes van luisboomsade (*Solanum mauritianum*) varieer baie en word beïnvloed deur die plek en seisoen van versameling. In die algemeen toon luisboomsade nie 'n primêre rus nie, maar omdat die vrugte dwarsdeur die jaar geproduseer word, is die meeste onderworpe aan weertoestande wat die sade tot 'n kondisionele dormansie kan laat oorgaan. Sade wat in die Natalse middelande versamel is, het 'n hoër frekwensie van kondisionele en sekondêre rus getoon as sade afkomstig van die ander lokaliteite. Ongeag die lokaliteit, is die hoogste sekondêre rus gevind wanneer sade gedurende die warmer maande versamel is. Baie sade sal dus die voor en/of na opkoms onkruiddoderbehandelings, wat normaalweg gedurende dié tydperk toegepas word, ontsnap.

Keywords: Bugweed, germination, seed dormancy, *Solanum mauritianum*.

Introduction

Solanum mauritianum Scop. (syn. *S. auriculatum* Ait.) originated in tropical South America (Symon 1981). In South Africa, this species, which is commonly known as bugweed, has become an important weed in pine plantations.

Bugweed is an opportunistic pioneer, and is seen in dense stands after clear-felling and in light gaps under a pine canopy. An important survival mechanism for plants growing under unpredictable conditions is the ability to develop seed variability or heteroblasty. Thus, even under optimum conditions, only a part of such a seed population will germinate at any one time. Each time that a stand of seedlings or older plants is destroyed, a new stand will soon arise from the seed bank to take its place (Cavers 1974).

Variation in germination behaviour between populations has been reported for a number of weed species (Cavers & Harper 1966; Naylor & Abdalla 1982; Froud-Williams 1987). This variation may be the result of environmental conditions during seed maturation, such as temperature and light, as in the case of *Solanum nigrum* L. Certain authors claim that constant temperatures favour germination whereas others maintain that alternating temperatures are required. Givelberg and Horowitz (1984) suggested that the apparently variable response to temperature may have arisen because seeds were of different origins. Place of harvest greatly influenced germination potential of *Dactylis glomerata* (Probert *et al.* 1985), *Cedrus deodara* (D. Don) G. Don. (Thapliyal & Gupta 1980), *Pinus taeda* L. (Richter & Switzer 1982), *Poa annua* L. and *Alopercus myosuroides* Huds. (Naylor & Abdalla 1982).

Germination of seed may also be influenced by season and year of harvest. This is the situation for *Spergula marina* (L.) Grisels, where germination at the optimum temperature and at different constant temperatures varied with the month of harvest (Okusanya & Ungar 1983). Variation was also found in *Amaranthus retroflexus* L., where seeds that matured in late autumn were less dormant than those that matured in late summer (Chadoeuf-Hannel & Barralis 1983).

Bugweed seeds, and those of other *Solanum* species, generally require both light and alternating temperatures for a good germination response (Campbell & Van Staden 1983). The seeds are thus conditionally dormant and germination can occur only when these requirements are met (Baskin & Baskin 1984). Application of gibberellic acid (GA_3) to bugweed seeds incubated under unfavourable conditions (constant temperatures in either the light or the dark) resulted in high germination percentages, provided that a threshold level of GA_3 was taken up by the seeds (Campbell & Van Staden 1983). Thus chemicals of a gibberellin-like nature may potentially be effective in the manipulation of germination for control purposes.

The aim of this study was to determine whether the germination requirements of bugweed seeds for light, alternating temperatures and GA_3 were influenced by origin and season of collection.

Materials and Methods

Harvesting and seed preparation

Seeds were harvested during autumn/mid-April; winter/mid-July; early summer/mid-November and late summer/mid-

February for two consecutive years. The four localities selected were: Groot Constantia in the Cape (34°02'S 18°25'E; altitude 107 m), Pretoria in the Transvaal (25°35'S 28°21'E; altitude 1164 m), Umdoni Park at the Natal South Coast (30°19'S 30°43'E; altitude 100 m), and Cedara State Forest in the Natal midlands (29°32'S 30°17'E; altitude 1076 m). Seeds from ripe fruits were cleaned by repeated washing in tap water. Those seeds that sank in water (viable seeds) (Campbell & Van Staden 1983) were air-dried and then stored in brown paper bags at room temperature until required for use. All germination experiments were initiated within one week of seed collection. Seeds from each locality were counted into groups of twenty and placed randomly into compartmentalized plastic trays/repli-dishes. There were six replicates of each treatment.

Growth regulator treatments

Solutions of 0, 100 or 500 mg l^{-1} GA_3 were added to the seeds in different compartments of repli-dishes and these were kept in the light or dark as required for each experiment. An aliquot of 1.5 ml of each treatment solution was added to each compartment.

Germination procedures

The plastic repli-dishes were placed in incubators at constant (20°C) or alternating (15/30°C) temperatures in the light or dark. All trays were exposed to 14 h light and 10 h dark in the incubators. Light was provided by 'cool white' fluorescent tubes (spectral irradiance 11 W m^{-2}). For dark germination, dishes were wrapped in two layers of aluminium foil, and the numbers of seeds that germinated were counted under a green safe light in a dark room. Germination was recorded weekly. Results are, however, expressed as final percentage germination after 12 weeks incubation. Subsequent to 12 weeks incubation, seeds were transferred to a second set of incubation conditions, for a further 12 weeks, as follows:

First incubation (12 weeks)	Second incubation (12 weeks)	Table
15/30°C Light	15/30°C Light	1
15/30°C Dark	15/30°C Light	2
20°C Dark	15/30°C Dark*	3
20°C Light	15/30°C Light	4 & 5

* After this incubation for 12 weeks, non-germinated seeds were transferred to conditions of 15/30°C in the light for a further 12 weeks.

Results

Primary dormancy

Bugweed seeds germinate readily at alternating temperatures of 15/30°C in the light. These temperatures have been described as optimum conditions for germination (Campbell 1991). Primary dormancy was not evident in most seed batches, regardless of season or year of collection, and high germination percentages occurred at optimum conditions (Table 1). On three occasions, however (April 1986, February 1987 and November 1987), Cedara seed batches reached significantly lower final germination percentages under optimum conditions than seed batches collected from the other sites. Thus, seeds shed at the Cedara site may sometimes exhibit partial primary dormancy (Table 1).

Conditional and secondary dormancy

Germination at alternating temperatures (15/30°C) in the dark

Seeds collected from Groot Constantia were most responsive to the above incubation conditions. Seeds collected from Cedara were only responsive if harvested during winter (July) (Table 2). Low final germination percentages occurred for all seed collected from Umdoni Park and in most batches from Pretoria. Thus, germination at 15/30°C in the dark was influenced by locality, season and year of collection.

Transfer of seed batches collected from Groot Constantia from dark incubation conditions to the light resulted in

Table 1 Germination of *Solanum mauritianum* at 15/30°C in the light. Seeds were harvested four times during the years 1986/87 and 1987/8. Results are presented as percentage germination (1) after 12 weeks and (2) after 24 weeks. Seeds were harvested from four localities: Cedara (Natal Midlands), Umdoni Park (Natal South Coast), Pretoria (Transvaal) and Groot Constantia (Cape). LSDs ($p < 0.05$) are presented for locality × season × year interactions

		Incubation conditions and locality							
		(1) Initial incubation conditions (15/30°C light for 12 weeks)				(2) Extended period at optimum conditions (15/30°C light for 24 weeks)			
Time of collection		Cedara	Umdoni Park	Pretoria	Cape	Cedara	Umdoni Park	Pretoria	Cape
April	1986	55	90	86	90	55	90	86	90
July	1986	70	79	78	88	86	83	90	88
November	1986	73	88	83	83	73	88	84	83
February	1987	47	72	75	82	49	78	79	82
April	1987	65	72	88	84	65	72	88	84
July	1987	86	74	90	84	86	74	90	84
November	1987	38	82	72	87	38	82	75	87
February	1988	74	73	79	85	74	73	79	85
		LSD $p < 0.05$ 20				LSD $p < 0.05$ 17			

moderate to high final germination percentages, indicating that in the dark, most of the non-germinated seeds had been in a state of conditional dormancy. This type of dormancy was also evident in most seed batches from Umdoni Park and Pretoria, except during November 1986, when less than half of the seeds germinated, and during February 1988, when transfer of seeds to the light did not promote further significant germination (Table 2). These seed batches with low germination were apparently no longer conditionally dormant and had entered secondary dormancy, which was induced by the initial unfavourable incubation condition of 15/30°C in the dark. The occurrence of secondary dormancy was most marked in seed batches from Cedara (Table 2).

Germination response of bugweed to constant temperatures (20°C) in the dark

No significant germination occurred under these unfavourable conditions, except in two seed batches from Groot Constantia, where a low but significant response was evident (Table 3). Transfer of non-germinated seeds to conditions of alternating temperatures in the dark showed an improved response in some seed batches but not in others (Table 3).

Table 2 Germination of *Solanum mauritianum* at 15/30°C in the dark. Seeds were harvested four times during the years 1986/7 and 1987/8. Results are presented as percentage germination (1) after incubation at 15/30°C in the dark for 12 weeks, and (2) 12 weeks after transfer to 15/30°C in the light. Seeds were harvested from four localities: Cedara (Natal Midlands), Umdoni Park (Natal South Coast), Pretoria (Transvaal) and Groot Constantia (Cape). LSDs ($p < 0.05$) are presented for locality × season × year interactions

		Incubation conditions and locality							
		(1) Initial incubation conditions (15/30°C dark for 12 weeks)				(2) Transfer to optimum conditions (15/30°C light for 12 weeks)			
Time of collection		Cedara	Umdoni Park	Pretoria	Cape	Cedara	Umdoni Park	Pretoria	Cape
April	1986	0	0	0	39	57	81	83	89
July	1986	32	10	17	66	73	85	56	89
November	1986	2	14	6	46	7	32	34	67
February	1987	0	0	0	49	9	90	58	63
April	1987	0	0	10	42	10	72	69	69
July	1987	69	8	11	18	90	86	79	87
November	1987	8	0	34	5	32	71	86	79
February	1988	7	0	15	7	7	3	21	56
		LSD $p < 0.05$ 19				LSD $p < 0.05$ 15			

Table 3 Germination of *Solanum mauritianum* at 20°C in the dark. Seeds were harvested four times during the years 1986/7 and 1987/8. Results are presented as percentage germination (1) after incubation at 20°C in the dark for 12 weeks, (2) 12 weeks after transfer to 15/30°C in the dark, and (3) 12 weeks after transfer to 15/30°C in the light. Seeds were harvested from four localities: Cedara (Natal Midlands), Umdoni Park (Natal South Coast), Pretoria (Transvaal) and Groot Constantia (Cape). LSDs ($p < 0.05$) are presented for locality × season × year interactions

		Incubation conditions and locality											
		(1) Initial incubation conditions (20°C dark for 12 weeks)				(2) Transfer to alternating temperature (15/30°C dark for 12 weeks)				(3) Transfer to optimum conditions (15/30°C light for 12 weeks)			
Time of collection		Cedara	Umdoni Park	Pretoria	Cape	Cedara	Umdoni Park	Pretoria	Cape	Cedara	Umdoni Park	Pretoria	Cape
April	1986	0	0	0	0	65	72	10	73	78	79	81	93
July	1986	0	0	0	0	86	84	74	90	86	84	74	90
November	1986	0	0	0	10	39	81	90	93	50	83	93	97
February	1987	0	0	0	1	10	78	76	74	12	80	78	76
April	1987	0	0	0	15	10	9	8	58	39	66	68	78
July	1987	2	0	0	3	10	4	0	20	17	82	80	98
November	1987	0	0	0	0	0	70	5	86	0	76	5	92
February	1988	0	0	0	3	10	6	26	45	21	92	92	70
		LSD $p < 0.05$ 3				LSD $p < 0.05$ 8				LSD $p < 0.05$ 8			

This indicated an end to conditional dormancy imposed during incubation at constant temperatures. A further transfer to the light (optimum conditions) promoted germination in some seed batches. Seeds from Groot Constantia, Pretoria and Umdoni Park were only rarely or never induced to enter secondary dormancy by incubation at constant temperatures in the dark. Transfer of seeds from Cedara, however, was not so effective, and several seed batches entered secondary dormancy (Table 3).

Germination responses of bugweed to constant temperatures (20°C) in the light

Germination of seeds from Cedara was generally very low at constant incubation temperatures, irrespective of season or year of collection. In contrast, seeds from the other sites showed a partial loss of the alternating temperature requirement for germination (Table 4). When seeds from these three sites were transferred from constant to alternating temperatures, germination was greatly enhanced, indicating

Table 4 Germination of *Solanum mauritianum* at 20°C in the light. Seeds were harvested four times during the years 1986/7 and 1987/8. Results are presented as percentage germination (1) after incubation at 20°C in the light for 12 weeks, and (2) 12 weeks after transfer to 15/30°C in the light. Seeds were harvested from four localities: Cedara (Natal Midlands), Umdoni Park (Natal South Coast), Pretoria (Transvaal) and Groot Constantia (Cape). LSDs ($p < 0.05$) are presented for locality × season × year interactions

		Incubation conditions and locality							
		(1) Initial incubation conditions (20°C light for 12 weeks)				(2) Transfer to optimum conditions (15/30°C light for 12 weeks)			
Time of collection		Cedara	Umdoni Park	Pretoria	Cape	Cedara	Umdoni Park	Pretoria	Cape
April	1986	0	8	0	5	84	80	70	87
July	1986	3	0	3	8	88	90	88	90
November	1986	0	0	4	31	85	90	88	90
February	1987	4	5	26	65	21	83	84	82
April	1987	11	45	86	49	77	71	86	73
July	1987	9	0	0	44	28	82	82	80
November	1987	5	6	0	15	79	81	83	86
February	1988	0	6	11	33	83	90	88	88
		LSD $p < 0.05$ 7				LSD $p < 0.05$ 8			

Table 5 Germination of *Solanum mauritianum* at 20°C in the light. Seeds were harvested four times during the years 1986/7 and 1987/8 and were incubated in 100 mg l^{-1} GA_3. Results are presented as percentage germination (1) after incubation at 20°C in the light for 12 weeks, and (2) 12 weeks after transfer to 15/30°C in the light. Seeds were harvested from four localities: Cedara (Natal Midlands), Umdoni Park (Natal South Coast), Pretoria (Transvaal) and Groot Constantia (Cape). LSDs ($p < 0.05$) are presented for locality × season × year interactions

		Incubation conditions and locality							
		(1) Initial incubation conditions (20°C light for 12 weeks)				(2) Transfer to optimum conditions (15/30°C light for 12 weeks)			
Time of collection		Cedara	Umdoni Park	Pretoria	Cape	Cedara	Umdoni Park	Pretoria	Cape
April	1986	41	76	76	81	87	77	76	81
July	1986	21	46	24	45	86	86	92	90
November	1986	36	66	70	56	87	85	85	77
February	1987	75	85	83	81	84	87	84	83
April	1987	59	71	88	90	81	80	88	90
July	1987	34	21	47	75	62	81	80	88
November	1987	59	73	86	87	77	73	86	87
February	1988	29	80	87	87	78	83	88	88
		LSD $p < 0.05$ 15				LSD $p < 0.05$ 14			

that the seeds had been in a state of conditional dormancy during incubation at constant temperatures (Table 4). However, secondary dormancy occurred in two seed batches from Cedara, and seeds no longer responded to optimum germination conditions (Table 4).

Temperature and secondary dormancy

To summarize, seeds collected at Groot Constantia showed the highest potential for germination under unfavourable conditions, and seldom entered secondary dormancy. In contrast, seeds from Cedara were the most exacting in their germination requirements and most readily entered secondary dormancy. It is probable that freshly-shed bugweed seeds will become shallowly buried rather than deeply buried and would therefore be subjected to alternating temperatures in the dark. These seeds may then be brought to the surface and be exposed to favourable conditions (alternating temperatures in the light), yet remain dormant. A consideration of secondary dormancy in Cedara and Groot Constantia seed batches induced by initial incubation at alternating 15/30°C in the dark is therefore given. The percentage of seeds that entered secondary dormancy following transfer to the light from conditions of 15/30°C in the dark was correlated (correlation coefficient, r) to the annual temperature cycle at Groot Constantia ($p < 0.01$) and was apparently inversely related to the annual rainfall cycle (Figure 1). The highest numbers of seeds entered secondary dormancy during the warmer drier months of the year (Figure 1).

Climatic conditions at Cedara are very different from those at Groot Constantia which has a winter rainfall climate. As with seeds from Groot Constantia, secondary dormancy was apparently correlated (r) to temperature, with a significance of $p < 0.05$ (Figure 2). However, higher percentages of seeds from Cedara entered secondary dormancy during the summer months than those collected at Groot Constantia. This might reflect a necessity to prevent germination during the onset of the harsher winters of this region (Figure 2).

The relationship between temperature and secondary dormancy in seeds from Umdoni Park and Pretoria was not significant. Peaks and troughs were displaced with respect to seasonal temperature fluctuations (results not shown). Nonetheless, peaks of secondary dormancy coincided approximately with peaks of high temperature. Other climatic factors at these sites probably interact to influence the development of secondary dormancy.

Effect of applying a below-threshold concentration of GA_3 (100 mg l^{-1}) on germination

Application of 100 mg l^{-1} GA_3 to the Cedara seed batches which showed a low germination response to optimum conditions (Table 1) broke their primary dormancy and germination was not significantly different from that of the other seed batches (results not shown). However, application of this level of growth regulator to seeds incubated under unfavourable conditions was variable, and dependent on incubation conditions:

- at 15/30°C in the dark, GA_3 substituted for a light requirement in all seed batches except one from Cedara (November 1986, Tables 1 and 2). In this case, conditional dormancy was not broken and seeds required the application of 500 mg l^{-1} GA_3 to prevent the induction of secondary dormancy;
- at 20°C in the dark, the effect of GA_3 was reduced, with only occasional substitution for a transfer requirement, and this depended on locality, season and year of collection. Application of 500 mg l^{-1} GA_3 completely substituted for this requirement, indicating that 100 mg l^{-1} GA_3 was below the threshold level for germination to occur (results not shown);
- a similar trend was obtained when seeds were incubated at 20°C in the light, since 100 mg l^{-1} GA_3 only partially substituted for the requirement for alternating temperatures. This was influenced by locality, season and year of collection (Tables 4 and 5). Application of 500 mg l^{-1} GA_3 to low-germinating seed batches broke conditional dormancy and completely substituted for the requirement of transfer to alternating temperatures (results not shown).

Thus, bugweed seeds show a variable response to the application of GA_3, and this appears to be influenced by locality, season and year of seed collection, and conditions of incubation.

Discussion

Generally, bugweed seeds do not exhibit primary dormancy. However, bugweed fruits are produced throughout the year (Campbell 1991) and most will be subjected to climatic conditions which make them conditionally dormant.

Shallowly buried seeds are exposed to diurnal temperature fluctuations/alternating temperatures (15/30°C) in the dark (Oke 1978; Campbell 1991). Under these conditions, seeds remain conditionally dormant in the soil. Soil disturbance may transfer seeds to the surface (light exposure), and certain seed batches have the capacity to germinate under these favourable conditions.

Deeply buried seeds are subjected to relatively constant temperatures in the dark (Oke 1978; Campbell 1991). When the soil is disturbed (thinning, felling operations), seeds may be brought nearer to the soil surface and may then be subjected to alternating temperatures in the dark, and may finally appear above the soil surface, where they will be exposed to light.

S. mauritianum seeds germinated poorly at constant temperatures in the dark, and either transfer to alternating temperatures (shallow burial) or a further transfer to the light (exhumation) was required before seeds germinated. Seed batches requiring both transfers were therefore in a deeper state of conditional dormancy than those requiring only a single transfer to alternating temperatures in the dark.

The germination response of seeds when incubated at constant temperatures in the light was highly variable. Certain seed batches germinated well under these conditions and had, therefore, lost their requirement for alternating temperatures. These seed batches had, therefore, lost conditional dormancy (Baskin & Baskin 1984) and a wider range of environmental conditions could be expected to result in germination. This variation in requirement for alternating temperatures was also seen in seeds of *S. nigrum*.

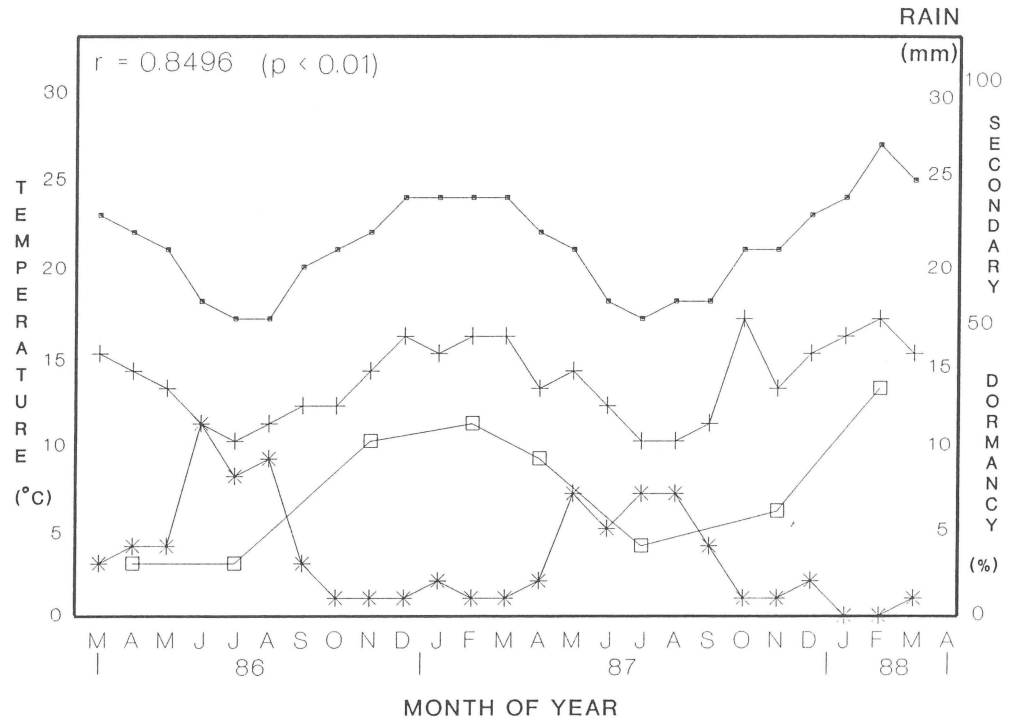

Figure 1 The relationship between monthly temperature or rainfall at Groot Constantia and percentage secondary dormancy of *Solanum mauritianum*, □—□. Maximum temperature (°C), □—□; minimum temperature (°C), +—+; rainfall (mm), ✳—✳.

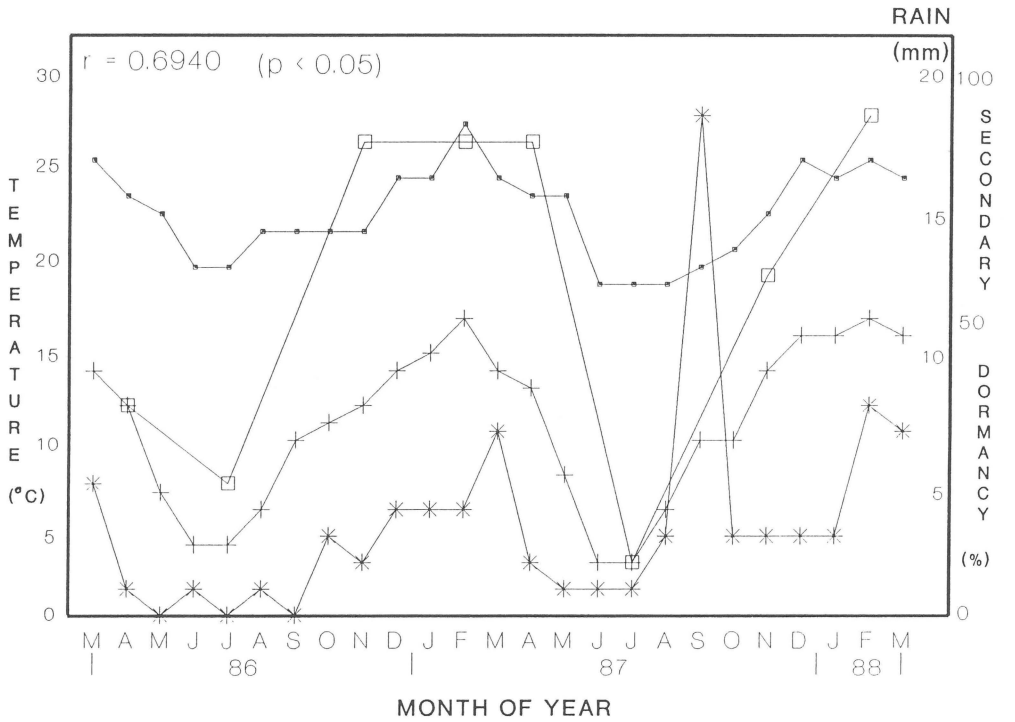

Figure 2 The relationship between monthly temperature or rainfall at Cedara and percentage secondary dormancy of *Solanum mauritianum*, □—□. Maximum temperature (°C), □—□; minimum temperature (°C), +—+; rainfall (mm), ✳—✳.

Givelberg & Horowitz (1984) suggested that the conflicting results recorded in the literature for *S. nigrum* were due to differences in localities of collection. This also appears to be true in the case of bugweed. The implications are that even under changed circumstances not all seeds will germinate, and a sporadic seedling emergence will occur over many seasons.

The occurrence of secondary dormancy was influenced by locality, season and year of collection as well as the type of unfavourable incubation conditions to which the seeds were initially subjected. Incubation at constant temperatures in the light only rarely induced secondary dormancy, in certain seed batches from Cedara. Incubation at both constant and alternating temperatures in the dark, however, resulted in a more frequent occurrence of secondary dormancy, especially in seeds from Cedara. Thus both shallowly buried seeds

(subject to alternating temperatures in the dark) and deeply buried seeds (subject to relatively constant temperatures in the dark) at Cedara will enter secondary dormancy, dependent on the season and year of harvest. Seeds from Cedara will thus be more difficult to control than those from the other sites, since a more sporadic seedling emergence will occur.

The occurrence of secondary dormancy was apparently influenced strongly by annual temperature. A large proportion of seeds shed at all sites during the warmer months of the year could therefore enter secondary dormancy, thereby escaping pre- and post-emergent herbicide treatments normally applied during this time.

A variable response to low concentrations of GA_3 was seen, depending on locality, season and year of collection. Application of 100 mg l^{-1} GA_3 had one of three effects: (a) it was sufficient to break primary dormancy in some seed batches, but was not required in others; (b) it was sufficient to break conditional dormancy under certain unfavourable incubation conditions but was below the threshold level required (500 mg l^{-1}) for other seed batches; or (c) it was sufficient to prevent certain seed batches entering secondary dormancy but was below the threshold level for others, which required 500 mg l^{-1} GA_3. Implications are that application to the soil seedbank of any growth regulator similar to GA_3 will prove ineffective in stimulating germination of all seeds.

Bugweed seed germination requirements are highly variable and change with locality, season and year of collection. This helps to explain why current control measures are failing to reduce the population in South Africa.

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